

# Comparison of measured and simulated growth on permanent plots in Sabah's rain forests

Peter Köhler\*, Thomas Ditzer\*, Robert C. Ong<sup>+</sup> and Andreas Huth\*

\* *Center for Environmental Systems Research, University of Kassel, Kurt-Wolters-Str. 3,  
D-34109 Kassel, Germany, Phone: +49 561 804 3175, Fax: +49 561 804 3176,  
email: koehler@usf.uni-kassel.de*

+ *Forest Research Centre, Forestry Department Sabah, P.O.Box 1407,  
90008 Sandakan, Sabah, Malaysia*

Version: 26th Januray 2000

## Abstract

In this paper previously unpublished field data from 25 ha of permanent sampling plots (PSPs) in Sabah, Malaysia, in four different forest reserves are analysed for mortality rates and basal area development. Field data of an observation length of nine to 20 years were available. These data then form the basis of several benchmark tests for the evaluation of the individual-oriented tropical rain forest growth model FORMIND . A new version of the FORMIND is presented. The model in its version FORMIND1.1 includes enhanced submodels for mortality and tree growth. The model evaluation is focused on the model components for tree growth, competition and mortality. Data for tree recruitment were not available. Results show a good agreement between simulation and field data for the main output variables basal area and stem number indicating a reasonable behaviour of the model components we focused on. Furthermore the results show that differences in site conditions influence tree growth and mortality. Site characteristics should be included in the model in the future.

Keywords: forest growth model; tropical rain forest; dipterocarp forest; mortality; Malaysia; basal area; FORMIND

*Forest Ecology and Management* (2001) 142(1-3): in press.

Copyrights ©2001 Elsevier Science B.V.

## 1 Introduction

Evaluation of forest growth models is an important procedure of model development. Vanclay and Skovsgaard (1997) discussed range and importance of model evaluation. An evaluation of tropical rain forest models is difficult due to a lack of adequate field data. Besides a comparison of model output in a steady state with primary rain forest data (e.g. Bossel and Krieger, 1994; Huth *et al.*, 1994, 1998; Kürpick *et al.*, 1997; Köhler and Huth 1998a, 1998b) few permanent sampling plot data exist which are suitable for testing rain forest growth models. The field data used in this paper were not available to the authors in times of model development and can therefore serve for testing of model results. Because those field data are used here for elaborating parameter values of mortality, they can not be seen as fully independent, but semi-independent.

The data used in the following were collected in the forest reserves Garinono, Gunung Rara, Segaliud Lokan and Sepilok in Sabah, Malaysia by the Forestry Department. Analysis in terms of site and stand characteristics, mortality and recruitment data are unpublished and only available in several research reports (Ong and Kleine, 1995; Köhler, 1998). Details of the field data used here are therefore documented in this paper. Especially mortality rates are analysed as a function of time and different plant functional types (PFTs).

Comparison of simulation results and field data from permanent sampling plots (PSPs) is important especially when models are used for estimation of long term trends of forest growth with or without anthropogenic influences as forest management (Huth *et al.*, 1994, 1998; Riswan and Hartanti, 1995) or climate change (Pastor and Post, 1988; Overpeck *et al.*, 1990; Shugart, 1998).

The simulation model investigated in this study is the tropical rain forest growth model FORMIND. FORMIND was developed following an individual-oriented approach (Huston *et al.*, 1988; Judson, 1994; Liu and Ashton, 1995; Uchmanski and Grimm, 1996) and used to validate the approach of the more aggregated process-based model FORMIX3 (Huth *et al.*, 1998). One important feature of both models is the use of species grouping into PFTs. A detailed model description and some results of FORMIND have already been presented in Köhler and Huth (1998a, 1998b). Several submodels (tree growth, competition, mortality) of FORMIND were modified in the meantime due to new available datasets, research activities and model analysis. These improvements are documented in the following.

## 2 Area description

The permanent sampling plots (PSPs) investigated in this study were established and inventoried by the Forest Research Centre and Forestry Department Sabah, Malaysia. They are all located in the lowland dipterocarp rain forest of Sabah, Malaysia. The PSPs located in different forest reserves across Sabah sum up to a forest area of 25 ha (see Table 1). The data set of Segaliud Lokan is split into two parts because of differing observation times within the forest reserve. The number of PSPs in the different locations varies from one to eleven ha, observation time from nine to 20 years with recordings in intervals between 1 and 5 years. Elevation is below 100 m, only Gunung Rara is located in a higher region (200 m - 600 m). Site quality was analysed by Ong and Kleine (1995) on the basis of landform and parent material. The site quality of Gunung Rara differs significantly from that of the other reserves.

Each PSP covers an area of 100 m  $\times$  100 m, subdivided into 25 patches of 20 m  $\times$  20 m, which are further split up into 4 sub-patches of 10 m  $\times$  10 m. Within these sub-patches no further information about tree location were recorded. Trees with a diameter at breast height (dbh)  $\geq$  10 cm are labelled. In regular inventories the dbh of all labelled trees were recorded including ingrowing small trees. Death of labelled trees was also recorded.

Display Table 1 around here.

## 3 Methods

### 3.1 The rain forest growth model FORMIND1.1

The FORMIND model was developed for the simulation of tropical rain forest in Malaysia (see Köhler and Huth, 1998a, 1998b for further details). It is a successor of the FORMIX3 model (Appanah *et al.*, 1990; Bossel and Krieger, 1991, 1994; Huth *et al.*, 1994, 1998). As main processes the model includes tree growth, competition, mortality and regeneration (last is not included in this version because of a lack of field data). In the following we will explain the approach used in version FORMIND1.1.

*Species grouping and spatial structure:* Tropical forest stands are usually composed of a large number of species. For the purpose of investigating forest dynamics it is useful to classify species into a small number of plant functional types (PFTs). Different concepts for PFTs were proposed (Swaine and Whitmore, 1988; Poker, 1993). We use three growth characteristics for grouping (potential height, light demands for growth and regeneration) and derive four PFTs for the dipterocarp lowland rain forests of Malaysia (Table 2, for details see Köhler and Huth, 1998b). A fifth PFT for bushes and small plants with heights below 1.3 m, which was used in former simulations (Köhler and Huth, 1998b) is not necessary here, because PSP inventories were focused on trees with a dbh  $\geq 10$  cm. For simulations a forest stand area of one hectare is divided into smaller patches. The model follows the gap-model approach (Botkin, 1972, 1993; Shugart, 1984) to modelling tree competition by describing tree interaction on patches. These patches have the size typical of treefall-gaps as they are naturally created by dying larger trees (20 m  $\times$  20 m), which is the same patch size as in the PSP inventories. In contrast to most gap-models (an exception is the ZELIG model by Smith and Urban, 1988; Urban *et al.*, 1991) we aim at picturing the shifting forest stand mosaic and we therefore simultaneously simulate several patches explicitly in their neighbouring location within the stand. The patches themselves are pictured as homogeneous.

Display Table 2 around here.

*Individual tree growth:* Within a single patch the model calculates the development of a forest stand based on cohorts of trees of the same PFT. Such a cohort is characterised by the number of trees and by the size of one representative tree. Using allometric relations, the size of a tree can equivalently be expressed in terms of its above-ground biomass, height, or diameter at breast height. The crown projection area is calculated from stem diameter via the proportionality of stem diameter and crown diameter (Rollet, 1978; Whitmore, 1984; Poker, 1993). These relationships between components of tree size (diameter, height and crown dimensions) are based on average field data, and are important simplifications that makes the model tractable, but they may reduce its accuracy. Emergent trees might have a crown projection area bigger than the patch size. Their crowns are then assumed to reach into the neighbouring four patches. Crown length is a function of tree height (Richards, 1952; Burgess, 1961; Poker, 1993). With these relations the distribution of individual tree crowns in the canopy can be calculated. Assuming a fixed leaf area index (LAI) of individual trees the leaf area distribution in the canopy can be calculated. The growth of the individual tree is based on a carbon balance. Calculations include photoproduction of the trees and assimilate losses due to respiration and renewal. Photoproduction is calculated from the tree's leaf area and its specific productivity. The latter depends on the local irradiance for each tree (Monsi and Saeki, 1953; Thornley, 1976). Within a patch light attenuation downwards in the canopy is calculated with respect to the absorption of higher located tree crowns. The dependence of specific photosynthetic productivity on irradiance is modelled using a Michaelis-Menten-type light response curve parametrised for each PFT (Eschenbach *et al.*, 1998). Assimilate losses are estimated in relation to tree biomass (Kira, 1978; Yoda, 1983). Losses are composed of renewal of roots, above-ground litter fall and of respiration of woody tree organs and of leaves. Respiration is considered a function of tree size and PFT (Ditzer, 1999). A water balance is not included in the model. The calculation of tree growth is performed in annual time steps.

*Competition:* Competition is modelled in terms of competition for light as described above and competition for space as described below concerning *mortality*.

1 *Mortality*: Mortality is modelled on an annual basis. In the current version it does not depend on  
 2 any other processes such as diameter increment. The mortality rates used for the simulations in this  
 3 study are directly obtained from the analysis of PSP-data. The model includes an additional crowding  
 4 mortality for trees in dense patches (crowns do not have enough space). In this case trees die to such  
 5 an extent that crowding does not occur anymore. Because of the short length of simulations ( $\leq 20$   
 6 years) we do not include processes of falling trees and the creation of canopy gaps by these trees.

7 *Regeneration*: The FORMIND model includes also a submodel for regeneration. Seedling establishment  
 8 was not measured in the PSPs. Estimation of recruitment rates as an alternative to the use of field  
 9 data is not considered, because uncertainties included in the estimation will lower the quality of the  
 10 evaluation. Therefore all tests are done without considering regeneration.

11 *Model parametrisation*: A detailed description of literature sources of the parameter values used for  
 12 the lowland dipterocarp rain forests of Sabah, Malaysia, is presented in Köhler and Huth, 1998b.  
 13 Table 3 contains the parametrisation used in the test undertaken for this paper. Values of parameters  
 14 in Table 3 are similar to those used in previous studies (Köhler and Huth, 1998a, 1998b) with the  
 15 exception of mortality rates (see Table 4), and the probability  $W$  of dying trees to fall.

Display Table 3 and Table 4 around here.

16 *Initialisation*: From the stem-diameter distribution of the first enumeration of each PSP trees are  
 17 aggregated into different cohorts regarding their PFT, diameter (in diameter classes with a width of  
 18 5cm) and location in the stand (in  $20 \text{ m} \times 20 \text{ m}$  patches).

## 19 3.2 Benchmark tests

20 As outlined by Vanclay and Skovsgaard (1997) a comparison of simulated data with field data not  
 21 used for model development is an appropriate method for evaluation of forest growth models called  
 22 benchmark test. Basal area and stem number were chosen for comparison of simulation results with  
 23 field data because these variables can directly be derived from the PSP inventory data. For each PSP  
 24 a simulation with FORMIND1.1 was performed over the same time period as data were available. In  
 25 cases where data of more than one hectare were available data were averaged after simulation. Two  
 26 different kinds of comparison were undertaken. First, basal area and stem number for different PFTs  
 27 at the end of the simulations were compared with those measured in the PSPs. Second, temporal  
 28 development of basal area and stem number over simulated/observed time was analysed.

29 We represent results in the following way:

$$30 \quad \frac{x_{\text{simulated}}(t_{\text{end}})}{x_{\text{measured}}(t_{\text{end}})} = f(x_{\text{measured}}(t_{\text{end}}), \text{PFT}, \text{FR}) \quad \text{and} \quad \frac{x_{\text{simulated}}}{x_{\text{measured}}} = f(t, \text{PFT}, \text{FR}), \quad (1)$$

31 with  $x$ : basal area or stem number,  $t_{\text{end}}$ : last year of inventory/simulation, FR: forest reserve,  $t$ : time  
 32 and PFT: plant functional type.

## 33 4 Results

### 34 4.1 Permanent sampling plot analysis

35 The structure and stocking of the PSPs varies widely as seen in Table 5. Where the stocking of  
 36 Segaliud Lokan2 and Gunung Rara is low (basal area (BA) of  $12.0$  and  $17.4 \text{ m}^2 \text{ ha}^{-1}$  respectively) the  
 37 relative fraction of pioneer species (PFT 3) is high indicating that these stands were heavily disturbed  
 38 by logging. In contrast, PSPs in Segaliud Lokan1, Garinono and Sepilok are well stocked (BA =  $31.3$ ,  
 39  $28.3$  and  $24.6 \text{ m}^2 \text{ ha}^{-1}$  respectively) with a lower fraction of pioneer species. Thus the data represent  
 40 a wide range of forest stocking.

Display Table 5 around here.

1 Annual mortality rates  $m$  were calculated in the following way (Manokaran and Swaine, 1994):  
 2  $m = (\log_e n_0 - \log_e n_1)/t$ , where  $n_0$  is the number of trees at the first enumeration,  $n_1$  is the  
 3 number of trees at the second enumeration  $t$  years later without considering any new trees growing in  
 4 between the two enumerations.

5 Mortality rates differ widely for different forest reserves. Table 4 lists average mortality rates for  
 6 different PFTs over the whole time of observation. Average values range from 0.24 %  $y^{-1}$  in Gunung  
 7 Rara to 6.34 %  $y^{-1}$  in Segaliud Lokan2. Mortality rates of pioneer species (PFT 3) are with the  
 8 exception of Gunung Rara generally higher than of non-pioneer species (e.g. Segaliud Lokan1:  $m =$   
 9 5.10 %  $y^{-1}$  for PFT 1,  $m = 12.03$  %  $y^{-1}$  for PFT 3). The time development of the average mortality  
 10 rates (Fig. 1) shows high fluctuations in most forest reserves. Especially in Gunung Rara, Segaliud  
 11 Lokan2 and Sepilok there is a constant increase in mortality rate to the end of the observation period.  
 12 In Segaliud Lokan2 a very high increase of the mortality rate was analysed ( $m = 0$  %  $y^{-1}$  for eight  
 13 years,  $m = 36$  %  $y^{-1}$  in the last year). Trends like this can not be explained with the present version  
 14 of the model which is based on constant mortality rates and therefore the last three years of data in  
 15 Segaliud Lokan2 are not considered in our tests.

Display Fig. 1 around here.

## 16 4.2 Evaluation of FORMIND1.1

17 In the simulation studies shown in this article we concentrate on the comparison of results with the  
 18 data from the permanent sampling plots. Other tests like the long term tendency of mature forest  
 19 stands incl. species composition were performed in Köhler and Huth (1998b).

20 The results of the benchmark tests following Eq. 1 are documented in Fig. 2. First we analyse the  
 21 results for the basal area, then the findings for the stem numbers.

Display Fig. 2 around here.

22 *Basal area (Fig. 2A&B):*

23 Simulations show a good agreement with the field observations. The deviation of simulation results  
 24 range between 0 % and 30 %, in only one case 50 %. There is no PFT where our simulations show  
 25 a trend of permanent over- or underestimation. PFT 1 seems to be the most critical PFT with the  
 26 highest deviation of nearly 50%. The highest deviation was observed for the forest reserve Gunung  
 27 Rara, which seems not to be simulated accurately with this version of the model. PFTs which have a  
 28 basal area below 5  $m^2 ha^{-1}$  tend to be simulated with lower values than measured. The total basal  
 29 areas are matching the measured values more precisely in stands with a higher stand basal area. Again  
 30 the highest variation is found in the Gunung Rara simulation.

31 Deviations in total basal area plotted against simulation/observation time show that nearly all forest  
 32 reserves stabilise within the simulation time at an acceptable error range ( $\pm 20\%$ ) with the exception  
 33 of Gunung Rara. Sepilok and Garinono come closer to measured values the longer we simulate.

34 *Stem number (Fig. 2C&D):*

35 Stem number can be simulated more precisely than basal area (maximum deviation: 25 %). This  
 36 is a result of the mortality rates used in the simulation which were derived from the observations  
 37 in the PSPs. The deviation of the total stem number after total simulated/observed time is in all  
 38 forest reserves below 6 %. There is a tendency of underestimating stem number in simulations. Again  
 39 deviation in plots with a higher stem number is smaller, highest deviation occurs from PFT 3, which  
 40 represent the pioneer species.

41 The deviation in total stem number plotted against simulation/observation time indicates always an  
 42 underestimation of simulated stem number. The deviation is stabilising with longer simulation time  
 43 for Sepilok from 10 % to nearly 0 %.

44 Results in stem number and basal area have to be analysed together. Development of stem number is  
 45 considered as a result of the simulated mortality processes, but the development of basal area is the

1 product of mortality, growth and competition processes in their interaction in a forest stand.

## 2 **5 Discussion**

### 3 **5.1 Mortality rates**

4 Typical values of the average tree mortality rates in primary tropical rain forests are 1-2 % of stem num-  
5 ber per year (Putz and Milton, 1982; Lang and Knight, 1983; Swaine *et al.*, 1987a, 1987b; Manokaran  
6 and Swaine, 1994; Milton *et al.*, 1994; Phillips and Gentry, 1994; Condit, 1995, 1998; Condit *et al.*,  
7 1995) with a significant higher mortality rate for pioneer species (Primack and Lee, 1991; Manokaran  
8 and Swaine, 1994). Manokaran and Swaine (1994) analysed mortality rates in secondary tropical rain  
9 forest and find no significant differences. The fact, that all our analysed average mortality rates do  
10 not fall in this range has to be discussed.

11 We did not consider ingrowth of trees after the first enumeration for the reason of evaluating our  
12 model without recruitment. This was also done assuming that the mortality rate for small trees with  
13 a dbh around 10cm does not differ from average mortality. The increasing mortality with time in  
14 three forest reserves indicates, that older trees might die faster than the average rate. However the  
15 typical fluctuations in mortality as seen in Garinono show no trend at all. Another reason for mortality  
16 increase might be an eight month long drought with no rainfall at all in the years 1982/83 in parts of  
17 Sabah (Leighton and Wirawon, 1986; Richards, 1996).

18 Gunung Rara's very low mortality of 0.25 %  $y^{-1}$  over ten years seems to be unrealistic. As mentioned  
19 earlier this forest reserves lies on poor sites and in higher elevation, and one might expect a mortality  
20 rate even higher than average. It might be that within the process of enumeration tree labels of  
21 dying trees were used several times leading to an underestimation of mortality rates. Mortality rate  
22 in Segaliud Lokan2, which was zero over eight years, seems reasonable, because of the small area of  
23 only 1 ha. On this scale extreme values might occur. Pioneer species show higher mortality rates as  
24 expected.

25 Even if the mortality rates are questionable in comparison with literature, they are a result of the data  
26 analysis of the PSPs and it is reasonable to use them as parameter values for simulations performed  
27 for benchmark testing.

### 28 **5.2 Model Evaluation**

29 The model in the here documented version is more complex in terms of competition and tree growth  
30 processes than most other rain forest growth model known to the authors (e.g. Kohyama, 1993; Ong  
31 and Kleine, 1995; Kürpick *et al.*, 1997; Huth *et al.*, 1998; Liu and Ashton, 1998). An exception is  
32 Chave (1999), who simulates spatial explicit tree positions for a rain forest in French Guiana. However  
33 one might find models for temperate forests (e.g. Bugmann, 1996) or even monocultures (e.g. Bossel,  
34 1996), which enhance certain features not included in FORMIND (e.g. soil properties, nutrient circles,  
35 weather, daily resolution, climate gradients). One might therefore think the model itself is simpler  
36 than today's forest growth models. For that reason we like to highlight the general differences in  
37 complexity between growth models for temperate and tropical forests and problems arising with a  
38 more detailed model structure. Beside the very high number of tree species in the tropics (over 400  
39 per hectare in Sabah) the unavailable data on those processes gives us very few arguments on how to  
40 parametrise them.

41 The spatial resolution used in the inventories (each PSP plot has an area of 1 ha divided in 25 patches  
42 of 20 m  $\times$  20 m) and in the model is the same. For that reason competition processes for light and  
43 space are simulated as accurate as possible in FORMIND. However nature is not as homogeneous in tree  
44 distribution as we assume in the model. Shading processes might therefore have a more significant

1 influence on individual tree growth. The aggregation of field inventory data into diameter classes  
2 with a width of 5cm as done in the initialisation results in slight overestimation of basal area at the  
3 beginning of the simulations (time = 0 a) as seen in Fig. 2.

4 The renunciation of using the recruitment submodel has only a small influence on the simulated stand  
5 dynamic, if short time scales are considered as in this paper. With the approximation of an upper  
6 diameter increment of  $1 \text{ cm y}^{-1}$  for non-pioneer species without light competition (Ong and Kleine,  
7 1995; Huth *et al.*, 1998) ingrowing trees with a dbh of 10 cm will not exceed a dbh of 30 cm within 20  
8 years. In all competition processes trees are only influencing other trees of approximately the same size  
9 or smaller. The ingrowth would, if activated, not effect the growth of the big trees in stand simulation  
10 and would therefore lead to only small differences in the simulated stand development. Because PSPs  
11 data were analysed without recruitment as well (only trees labelled during first enumeration were  
12 considered further), accuracy of the comparison should not be weakened.

13 Considering mortality without the process of falling trees influences only the spatial distribution of  
14 tree mortality. Because mortality effects of gap creating falling tree are implicitly included in the field  
15 data, average mortality is parametrised correctly. Locally high mortality rates would effect recruitment  
16 pattern in this area, but may be ignored due to inactive recruitment submodel.

17 Applying the model with four of the five PFT, as indicated in the model description, has no effects  
18 on model results. As only trees with a dbh  $\geq 10$  cm are considered in the results, these fifth PFT  
19 would not change simulated basal area or stem number directly, trees of the fifth PFT have a maximum  
20 diameter of 2 cm. Only consequences might be indirect competition effects on small ingrowing saplings  
21 of other PFTs.

22 The fixed geometric relations between different variables like tree height and crown length in the model  
23 do not allow the trees to adapt crown structures to their specific individual environment. Crowns might  
24 overlap with those of neighbouring trees in dense patches. Therefore crowding mortality is needed as a  
25 regulating process. This is an additional mortality which leads to a constant underestimation of stem  
26 numbers. Simulations without this regulation end with higher deviation in basal area from measured  
27 data. The process of crowding mortality covers only a small part of the total mortality (0.05-0.25 %  
28 out of 2-5 %) but is important for a realistic simulation of basal area.

29 The simulations for Gunung Rara fit worst with field data. These deviations might be caused by the  
30 higher elevation and poor site conditions in Gunung Rara. Conditions found in Gunung Rara fall  
31 out of the present application range of FORMIND1.1. However with a more detailed description of  
32 individual tree growth as a function of site conditions FORMIND has the potential to simulate stands  
33 like Gunung Rara with similar accuracy as the other forest reserves.

34 To exclude data of the last years in Segaliud Lokan2 form further testing was reasoned with the small  
35 spatial scale of only 2 ha and the large temporal differences in mortality rates ( $0.0 \text{ \% y}^{-1}$  for first years  
36 and rates between 20 and 40%  $\text{y}^{-1}$  in the last years). We think errors in field measurements might be  
37 one reasons for the unexpected data. Additionally, as our main objective in this benchmark testing  
38 was to validate our growth model an assumed average mortality for the whole observation time  $\neq 0.0$   
39  $\text{\% y}^{-1}$  in Segaliud Lokan2 would cover tree growth effects.

40 The good agreement between simulation and field data are first hints that FORMIND1.1 is an adequate  
41 tool to simulate the growth of tropical rain forest not only on a short time scale of some decades but  
42 also for long time forest development. Results over simulation periods of 100 years and more were  
43 already published in Köhler and Huth (1998a, 1998b).

44 Given the wide variation in calculated mortality rates, one might ask how save is it to use an average  
45 or published rate to predict forest development. With a sensitivity analysis, which highlights the  
46 influences of different parameters, the importance of mortality and acceptable parameter ranges can  
47 be analysed (Huth *et al.*, 1998). Investigations show, that mortality is important for model behaviour,  
48 but parameter values might vary reasonable without changing results in general. Thus, to use more  
49 general independent data for benchmark testing, might influence the accuracy only slightly.

1 Because of the variety of different stockings represented in the PSPs the tests show that FORMIND1.1  
2 is applicable within good site conditions on every possible level of forest degradation. Tests shown  
3 in this paper together with results for the simulation of primary forest (Köhler and Huth 1998a,  
4 1998b) evaluate it as an accurate tool for estimating the effects of logging operations on tropical forest  
5 ecosystems (future work).

## 6 **6 Conclusion**

7 Beside Ong and Kleine (1995) and Liu and Ashton (1998), which all used data from permanent  
8 sampling plots to parametrise their models a detailed comparison of growth data with model results  
9 was not performed so far. A comparison is limited to the quality and observation period of available  
10 data sets and therefore the case study in this paper is limited to time periods up to twenty years  
11 without considerations of regeneration. However, for the development of models, which estimate long  
12 term tendencies in tropical rain forests with and without antropogeneous influences even those limited  
13 data are of importance for model evaluation. Thus, the benchmark tests gave us indications, where  
14 the limits of model application are. Only with this knowledge an application of forest growth models  
15 to questions of management practise becomes viable.

## 16 **Acknowledgement**

17 We like to thank the Forest Research Centre, the Forestry Department Sabah, Malaysia, and the  
18 Malaysian-German Sustainable Forest Management Project and their members, especially M. Kleine.  
19 Thanks to R. Glauner for coordinating between Malaysian and German projects. Parts of the work  
20 for this paper were supported by the Deutsche Forschungsgemeinschaft (DFG). We also owe thanks  
21 to two anonymous reviewer, who gave critical but very useful comments.

## 22 **References**

- 23 Appanah, S., Weinland, G., Bossel, H., Krieger, H., 1990. Are tropical rain forests non-renewable?  
24 An enquiry through modelling. *J. Trop. For. Sci.* 2(4), 331-348.
- 25 Bossel, H., 1996. TREEDYN3. A forest simulation model. *Ecol. Model.* 90, 187-227.
- 26 Bossel, H., Krieger, H., 1991. Simulation model of natural tropical forest dynamics. *Ecol. Model.*  
27 59, 37-71.
- 28 Bossel, H., Krieger, H., 1994. Simulation of multi-species tropical forest dynamics using a vertically  
29 and horizontally structured model. *For. Ecol. Manage.* 69, 123-144.
- 30 Botkin, D.B., 1993. *Forest dynamics: An ecological model.* Oxford University Press, Oxford.
- 31 Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of  
32 forest growth. *J. Ecol.* 60, 849-872.
- 33 Bugmann, H.K.M., 1996. A simplified forest model to study species composition along climate  
34 gradients. *Ecology* 77, 2055-2074.
- 35 Burgess, P.F., 1961. The structure and composition of lowland tropical rain forest in North Borneo.  
36 *Malays. For.* 1, 24, 66-80.
- 37 Chave, J., 1999. Study of structural successional and spatial pattern in tropical rain forests using  
38 TROLL a spatially explicit forest model. *Ecol. Model.* 124, 233-254.



- 1 Condit, R., 1995. Research in large, long-term tropical forest plots. *TREE* 10(1), 18-21.
- 2 Condit, R., 1998. Tropical forest census plots: methods and results from Barro Colorado Island,  
3 Panama and a comparison with other plots. Springer, Berlin.
- 4 Condit, R., Hubbell, S.P., Foster, R.B., 1995. Mortality rates of 205 neotropical tree and shrub  
5 species and the impact of a severe drought. *Ecol. Monogr.* 65(4), 419-439.
- 6 Ditzer, T., 1999. Struktur und Dynamik natürlicher und bewirtschafteter Dipterocarpaceenwälder:  
7 Eine Fallstudie der Modellbildung und Simulation für die Bewirtschaftung natürlicher  
8 Ressourcen unter Unsicherheit. Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen  
9 und Subtropen 131, Verlag Erich Goltze, Göttingen, Germany.
- 10 Eschenbach, C., Glauner, M., Kleine, M., Kappen, L., 1998. Photosynthesis rates of selected tree  
11 species in lowland dipterocarp rain forests of Sabah, Malaysia. *Trees* 12, 356-365.
- 12 Huston, M, DeAngelis, D., Post, W., 1988. New computer models unify ecological theory. *BioScience*  
13 10(38), 682-691.
- 14 Huth, A., Ditzer, T., Bossel, H., 1998. The rain forest growth model FORMIX3 - model description and  
15 analysis of the forest growth and logging scenarios for the Deramakot forest reserve, Malaysia.  
16 Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen 124, Erich  
17 Goltze Verlag, Göttingen, Germany.
- 18 Huth, A., Hahn-Schilling, B., Bossel, H., 1994. Untersuchungen der Auswirkungen von verschiedenen  
19 Nutzungsstrategien auf das Wachstum von Moorregenwald - Simulationen mit FORMIX3. *Z.*  
20 *Ökologie u. Naturschutz* 3, 217-225.
- 21 Judson, O.P., 1994. The rise of the individual-based model in ecology. *TREE* 9, 9-14.
- 22 Kira, T., 1978. Community architecture and organic matter dynamics in tropical lowland rain  
23 forests of Southeast Asia with special reference to Pasoh Forest, West-Malaysia. In: Tomlinson,  
24 P.B., Zimmermann, M.H. (Eds.), *Tropical Trees as Living Systems*. Proceedings, 4th Cabot  
25 Symposium, Harvard Forest, University Press, Cambridge, Mass., pp 26-30.
- 26 Köhler, P., 1998. Parameter research for the tropical rain forest growth model FORMIX 4. Center for  
27 Environmental Systems Research, University of Kassel, Kassel, Report P9801.
- 28 Köhler, P., Huth, A., 1998a. An individual based rain forest model - concepts and simulation  
29 results. In: Kastner-Maresch, A., Kurth, W., Sonntag, M., Breckling, B. (Eds.), *Individual-based*  
30 *structural and functional models in ecology*. Bayreuther Forum Ökologie, Vol. 52, Bayreuther  
31 Institut für terrestrische Ökosystemforschung, Bayreuth, pp 35-51.
- 32 Köhler, P., Huth, A., 1998b. The effects of tree species grouping in tropical rain forest modelling -  
33 simulations with the individual based model FORMIND . *Ecol. Model.* 109, 301-321.
- 34 Kohyama, T., 1993. Size-structured tree populations in gap-dynamic forest. The forest architecture  
35 hypothesis for the stable coexistence of species. *J. Ecol.* 81, 131-143.
- 36 Kürpick, P., Kürpick, U., Huth, A., 1997. The influence of logging on a Malaysian Dipterocarp rain  
37 forest: a study using a forest gap model. *J. theor. Biol.* 185, 47-54.
- 38 Lang, G.E., Knight, D.H., 1983. Tree growth, mortality, recruitment, and canopy gap formation  
39 during a 10-year period in a tropical moist forest. *Ecology* 64, 1075-1080.
- 40 Leighton, M., Wirawan, N., 1986. Catastrophic draught and fire in Borneo tropical rain forest  
41 associated with the 1982-1983 El Niño southern oscillation event. In: Prance, G.T. (Ed.),  
42 *Tropical rain forests and world atmosphere*. Westview, Boulder, pp 75-102.

- 1 Liu, J., Ashton, P.S., 1995. Individual-based simulation models for forest succession and management.  
2 For. Ecol. Manage. 73, 157-175.
- 3 Liu, J., Ashton, P.S., 1998. FORMOSAIC: an individual-based spatially explicit model for simulating  
4 forest dynamics in landscape mosaics. Ecol. Model. 106, 177-200.
- 5 Manokaran, N., Swaine, M.D., 1994. Population Dynamics of Trees in Dipterocarp Forests of Penin-  
6 sular Malaysia. Malayan Forest Records No. 40, Forest Research Institute Malaysia.
- 7 Milton, K., Laca, E.A., Demment, M.W., 1994. Successional pattern of mortality and growth of large  
8 trees in a Panamanian lowland forest. J. Ecol. 82, 79-87.
- 9 Monsi, M., Saeki, T., 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung  
10 für die Stoffproduktion. Jap. J. Bot. 14, 22-52.
- 11 Ong, R.C., Kleine, M., 1995. DIPSIM: A dipterocarp forest growth simulation model for Sabah.  
12 FRC Research Papers 2, Forestry Department, Sabah, Malaysia.
- 13 Overpeck, J.T., Rind, D., Goldberg, R., 1990. Climate-induced changes in forest disturbance and  
14 vegetation. Nature 343, 51-53.
- 15 Pastor, J, Post, W.M., 1988. Response of northern forests to CO<sub>2</sub>-induced climate change. Nature  
16 334, 55-58.
- 17 Phillips, O.L., Gentry, A.H., 1994. Increasing turnover through time in tropical forests. Science 263,  
18 954-958.
- 19 Poker, J., 1993. Struktur und Dynamik des Bestandesmosaik tropischer Regenwälder Mitteilungen  
20 der Bundesanstalt für Forst- und Holzwirtschaft, Nr. 174, Wiedebusch Verlag, Hamburg.
- 21 Primack, R.B., Lee, H.S., 1991. Population dynamics of pioneer (*Macaranga*) trees and understorey  
22 (*Mallotus*) in selectively logged Bornean rain forests. J. of Trop. Ecol. 7, 439-458.
- 23 Putz, F.E., Milton, K., 1982. Tree mortality rates on Barro Colorado Island. In: Leigh, E.G.jr.,  
24 Rand, A.S., Windsor, D.M. (Eds.), The ecology of a tropical forest. Smithsonian Institution  
25 Press, Washington DC. pp 95-100.
- 26 Richards, P.W., 1952. Tropical rain forest. Cambridge University Press, Cambridge.
- 27 Richards, P.W., 1996. The tropical rain forest - an ecological study. Cambridge University Press,  
28 Cambridge.
- 29 Riswan, S. Hartanti, L., 1995. Human impacts on tropical forest dynamics. Vegetatio 121, 41-52.
- 30 Rollet, B., 1978. Organisation. In: UNESCO, UNEP, FAO (Eds.), Tropical forest ecosystems. A  
31 state of knowledge report. UNESCO-UNEP, Paris, pp 112-142.
- 32 Shugart, H.H., 1984. A theory of forest dynamics. Springer, New York.
- 33 Shugart, H.H., 1998. Terrestrial ecosystems in changing environments. Cambridge University Press,  
34 Cambridge.
- 35 Smith, T.M., Urban, T.L., 1988. Scale and resolution of forest structural pattern. Vegetatio 74,  
36 143-150.
- 37 Swaine, M.D., Whitmore, T.C., 1988. On the definition of ecological species groups in tropical rain  
38 forests. Vegetatio 75, 81-86.
- 39 Swaine, M.D., Hall, J.B., Alexander, I.J., 1987a. Tree population dynamics at Kasde, Ghana (1982-  
40 1986). J. Trop. Ecol. 3, 331-345.

- 1 Swaine, M.D., Lieberman, D., Putz, F.E., 1987b. The dynamics of tree populations in tropical forest:  
2 a review. *J. Trop. Ecol.* 3, 359-366.
- 3 Thornley, J.H.M., 1976. *Mathematical models in plant physiology*. Academic Press, New York.
- 4 Uchmanski, J., Grimm, V., 1996. Individual-based modelling in ecology: what makes the difference?  
5 *TREE* 11(10), 437-441.
- 6 Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models.  
7 *For. Ecol. Manag.* 42, 95-110.
- 8 Vanclay, J.K., Skovsgaard, J.P., 1997. Evaluating forest growth models. *Ecol. Mod.* 98, 1-12.
- 9 Whitmore, T.C., 1984. *tropical rain forest of the far east*. Oxford Science, Oxford.
- 10 Yoda, K., 1983. Community respiration in a lowland rain forest in Pasoh, Peninsular Malaysia. *Jap.*  
11 *J. Ecol.* 33, 183-197.

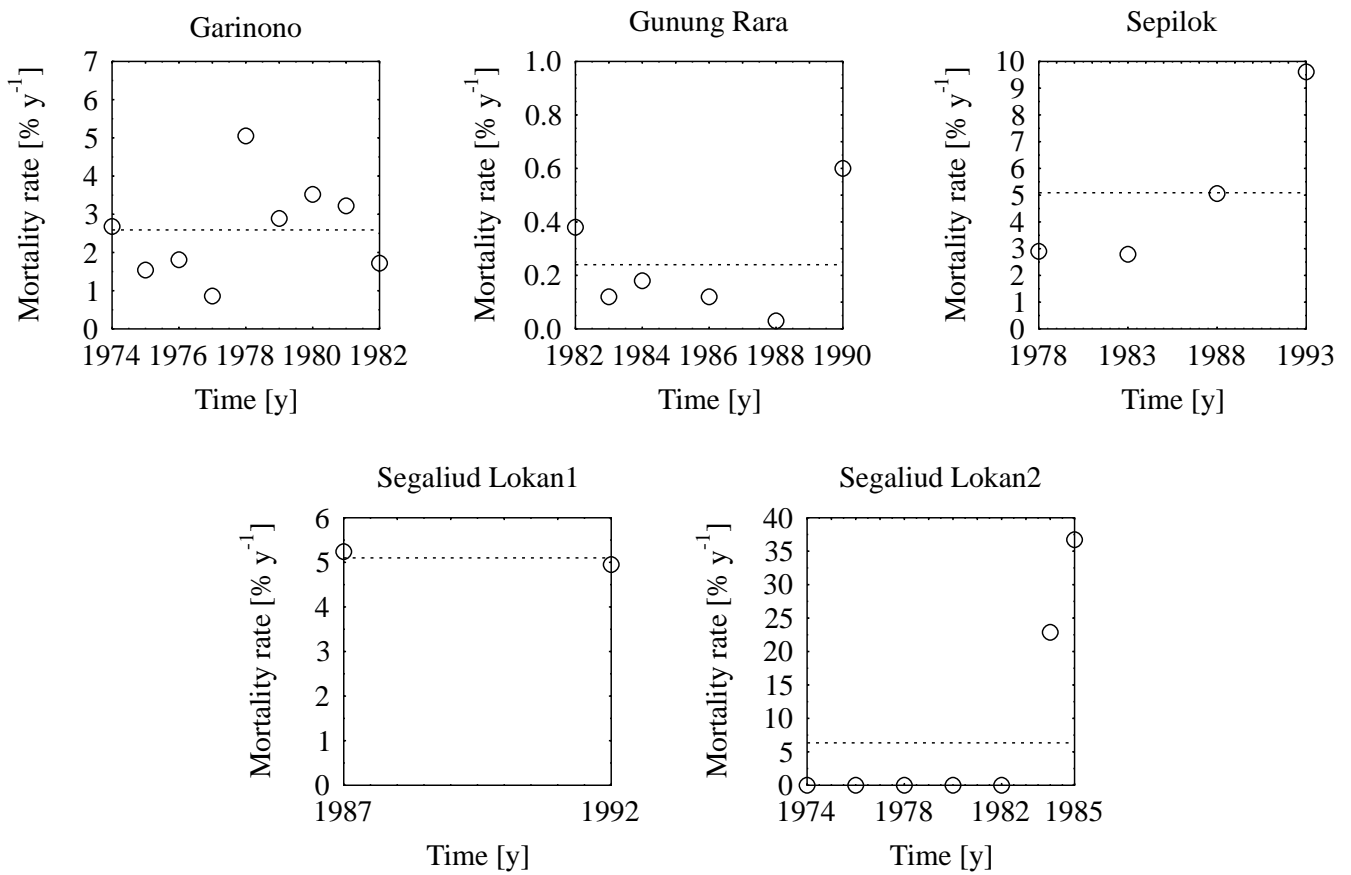


Figure 1: Mortality rates as function of time in permanent sampling plots (PSPs) in different locations (Garinono, Gunung Rara, Segaliud Lokan and Sepilok) in Sabah. Detailed information about PSPs in Table 1. Dotted Line: Average mortality rate between first and last enumeration. Circles: Mortality rate between actual and previous enumeration. Circles also describe when enumerations took place.

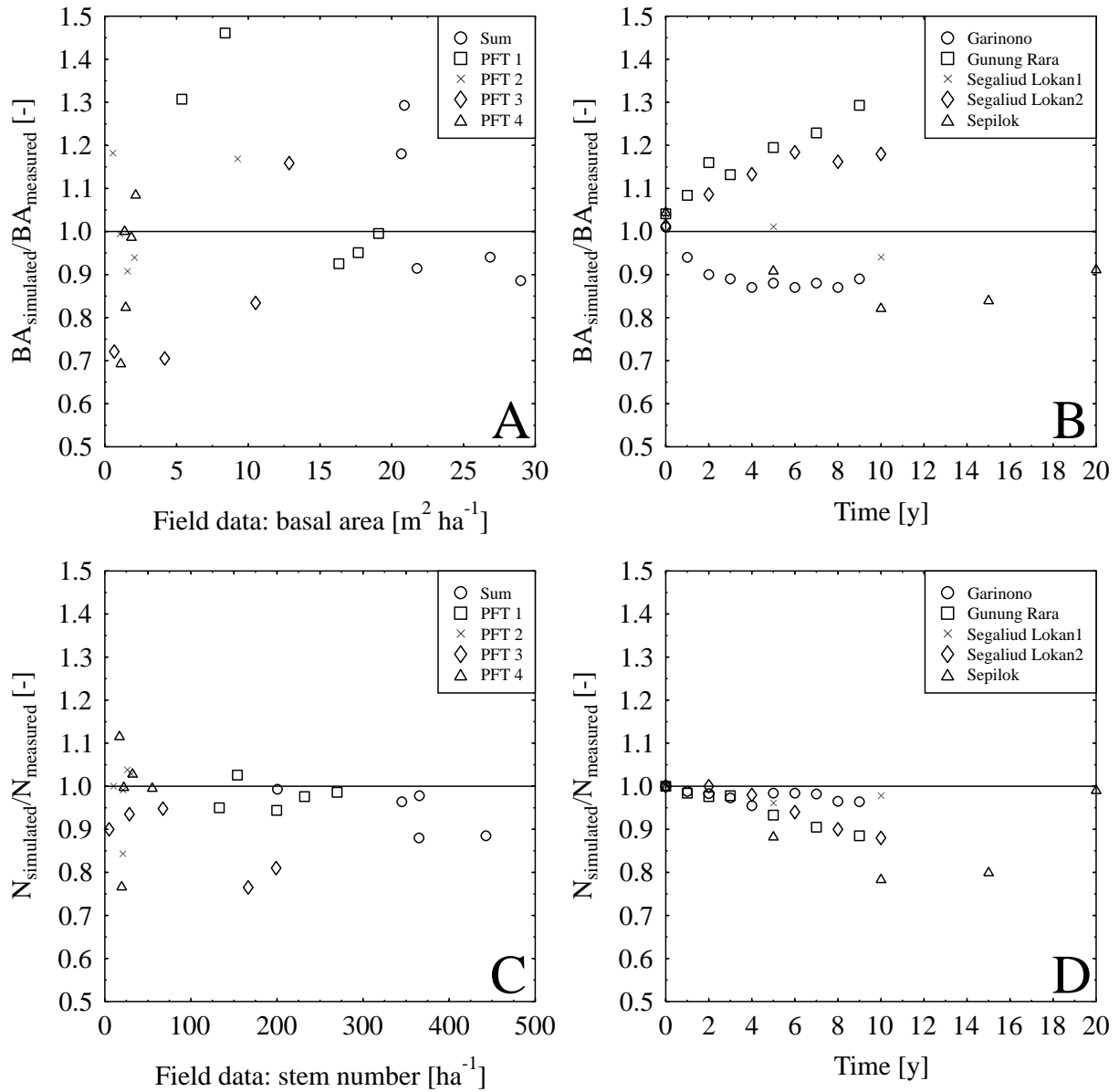


Figure 2: Benchmark tests. Relative variation in basal area BA (A, B) and stem number N (C, D) of simulation against field data. A, C: Final variation after maximum simulation time (= length of observation) as a function of field measurement in last enumeration. For each of the permanent sampling plots (PSPs) data for each plant functional type PFT 1-4 and sum are plotted. B, D: Variation as function of simulation/observation time. Plotted are total basal areas and total stem numbers for PSPs in Garinono, Gunung Rara, Segaliud Lokan and Sepilok. For information on PSPs see Table 1.

Table 1: Information about permanent sampling plots (PSPs) located in different forest reserves in Sabah, Malaysia. A: size of PSPs [ha]; B: number of trees at first enumeration; C: time of observation; D: length of observation [y]; E: number of enumerations; F: time between two enumerations [y]; G: time between last logging and first inventory [y]; H: site quality.

Location	A	B	C	D	E	F	G	H	Elevation [m]
Garinono	2	871	1973-1982	9	10	1	45	good	40-80
Gunung Rara	11	4978	1981-1990	9	7	1-2	11-12	poor	200-600
Segaliud Lokan1	7	4258	1982-1992	10	3	5	25	good	40-100
Segaliud Lokan2	1	365	1972-1985	13	8	1-2	8	good	40-100
Sepilok	4	2218	1973-1993	20	5	5	19	good	20-50

Table 2: Characteristics of the aggregated plant functional types (PFTs) of lowland dipterocarp rain forest of Sabah, Malaysia.

PFT	Maximum heights	Light demand	Species composition
1	>36 m	shade tolerant emerging species	mainly dipterocarps
2	25-36 m	shade tolerant climax species	dipterocarps and non-dipterocarps
3	15-25 m	light demanding pioneer species	mainly <i>Macaranga spp.</i> and <i>Antocephalus chinensis</i>
4	≤15 m	shade tolerant understorey species	non-dipterocarps

Table 3: Parametrisation for a dipterocarp lowland rain forest in Sabah, Malaysia, used by the FORMIND1.1 model. Parameters concerning mortality are depending on the location and can be found in Table 4. Names are identical to those used in the detailed model description in Köhler and Huth (1998b). Index  $j$  indicates that parameter values differ for different plant functional types.

Name	Description	Unit	Plant functional type			
			1	2	3	4
$a_{0j}$	Coefficient of height-diameter relation <sup>a</sup>	[m]	2.94	2.30	1.97	3.11
$a_{1j}$	Coefficient of height-diameter relation	[m cm <sup>-1</sup> ]	0.42	0.42	0.39	0.30
$a_{2j}$	Coefficient of height-diameter relation	[m cm <sup>-2</sup> ]	-0.002	-0.002	-0.002	-0.001
$\rho_j$	Wood density	[t <sub>odm</sub> m <sup>-3</sup> ]	0.62	0.57	0.37	0.71
$h_{Mj}$	Maximum potential height	[m]	55	36	25	15
$P_{Mj}$	Maximum photo-productivity	[ $\frac{\text{mgCO}_2}{\text{dm}^2 \cdot \text{h}}$ ]	10.9	11.6	29.1	18.8
$\alpha_j$	Slope of light response curve	[ $\frac{\text{mgCO}_2 \cdot \text{m}^2}{\text{dm}^2 \cdot \text{h} \cdot \text{W}}$ ]	0.36	0.20	0.20	0.30
$\tau_j$	Fraction of stemwood to total biomass	[-]	0.7			
$s_j$	Crown-to-stem-diameter-ratio	[-]	25			
$LAI_j$	Leaf area index of single tree	[-]	2			
$R_{Pj}$	Respiration (biomass losses relative to above ground biomass)	[y <sup>-1</sup> ]	0.16			
$I_0$	Light intensity above canopy	[W m <sup>-2</sup> ]	335			
$k$	Light extinction coefficient	[-]	0.7			
$W$	Probability for a dying tree to fall	[-]	0.0			

<sup>a</sup>Height-diameter relation:  $h = a_{0j} + a_{1j} \cdot d + a_{2j} \cdot d^2$ .

Table 4: Average mortality rate  $m$  [% y<sup>-1</sup>] for different plant functional types calculated from permanent sampling plot data in different locations and used as parameter values for simulations. For Segaliud Lokan2 we only used the data recorded between 1972-1982 and the parameter values used in simulations therefore differ from the average value.

Location	average	Plant Functional Type			
		1	2	3	4
Garinono	2.59	2.40	0.62	3.86	2.54
Gunung Rara	0.24	0.31	0.26	0.12	0.16
Segaliud Lokan1	5.10	4.48	2.89	12.03	3.46
Segaliud Lokan2	(6.34)	0.0	0.0	0.0	0.0
Sepilok	5.09	5.49	3.76	5.89	2.58

Table 5: Basal area (BA) and stem number of all species ( $N_{\text{all}}$ ) and the different plant functional types ( $N_1, N_2, N_3, N_4$ ) at the beginning of observation for trees with  $d \geq 10\text{cm}$  in different forest reserves.

Location	BA [m <sup>2</sup> ha <sup>-1</sup> ]	$N_{\text{all}}$ [ha <sup>-1</sup> ]	$N_1$ [ha <sup>-1</sup> ]	$N_2$ [ha <sup>-1</sup> ]	$N_3$ [ha <sup>-1</sup> ]	$N_4$ [ha <sup>-1</sup> ]
Garinono	28.3	435.5	288.0	27.5	95.5	24.5
Gunung Rara	17.4	450.4	205.9	21.6	168.6	56.0
Segaliud Lokan1	31.3	608.3	422.4	41.0	95.1	45.4
Segaliud Lokan2	12.0	365.0	133.0	10.0	199.0	22.0
Sepilok	24.6	554.5	462.0	44.0	16.3	28.5